

1 **Running title:** Global biocrusts distribution

2 **Advancing studies on global biocrusts distribution**

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17

18 **Abstract:** Biological soil crusts (biocrusts hereafter) cover a substantial proportion of the
19 dryland ecosystem and play crucial roles in ecological processes such as biogeochemical cycles,
20 water distribution, and soil erosion. Consequently, studying the spatial distribution of biocrusts
21 holds great significance for drylands, especially on a global scale, but it still needs to be
22 improved. This study aimed to stimulate global-scale investigations of biocrust distribution by
23 introducing three major approaches: spectral characterization indices, dynamic vegetation
24 models, and geospatial models while discussing their applicability. We then summarized the
25 present understanding of the factors influencing biocrust distribution. Finally, to further
26 advance this field, we proposed several potential research topics and directions, including the
27 development of a standardized biocrust database, enhancement of non-vascular vegetation
28 dynamic models, integration of multi-sensor monitoring, extensive use of machine learning,
29 and a focus on regional research co-development. This work is supposed to significantly
30 contribute to mapping the biocrust distribution and thereby advance our understanding of
31 dryland ecosystem management and restoration.

32 **Key words:** biological soil crusts; distribution; drylands; global scales; regional scales

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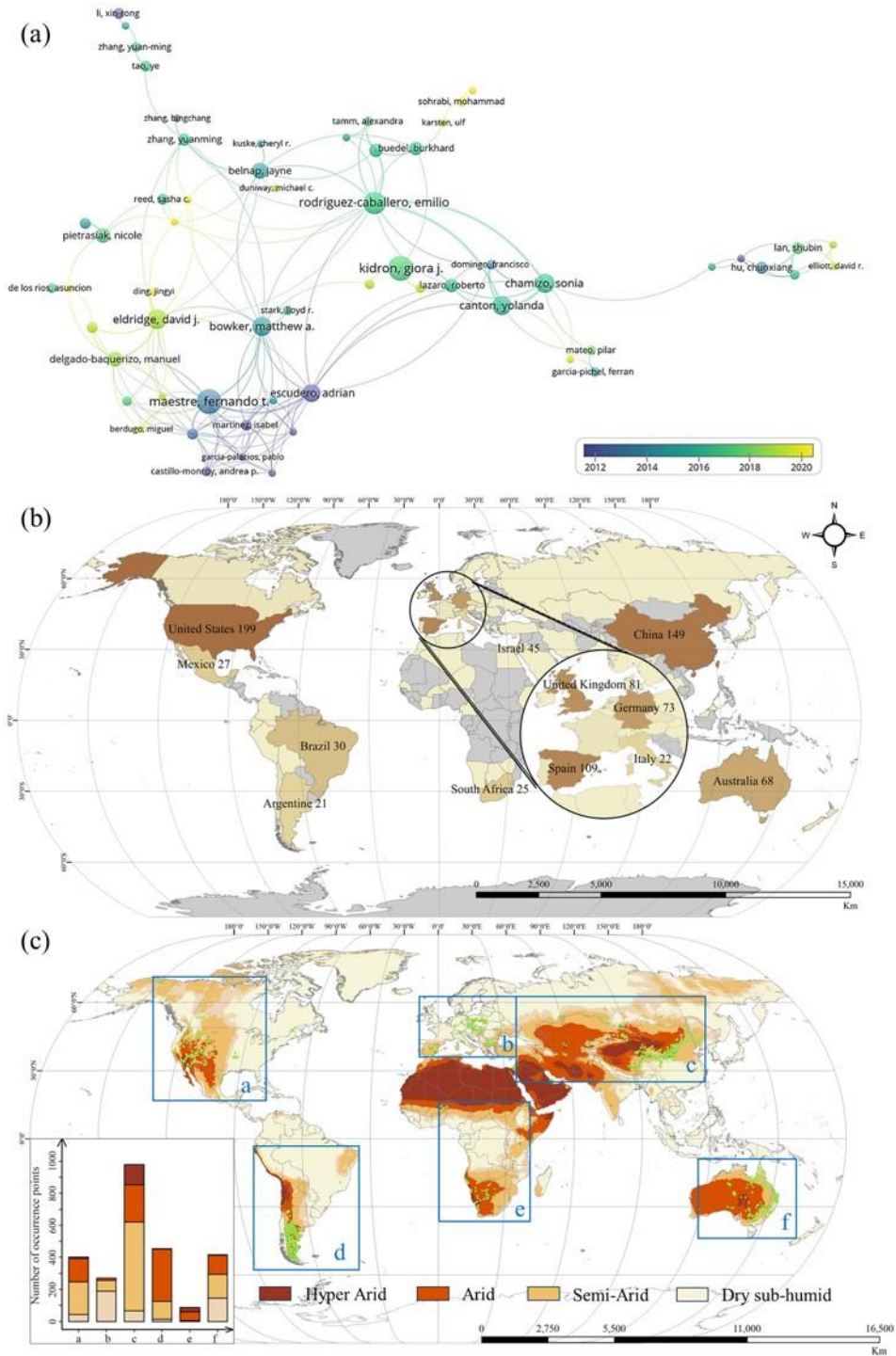
34 **1. Introduction**

35 Biological soil crusts (biocrusts hereafter) are continuous biotic complexes that live in the
36 topsoil, which are formed by different proportions of photosynthetic autotrophic (e.g.
37 cyanobacteria, algae, lichens, mosses) and heterotrophic (e.g. bacteria, fungi, archaea)
38 organisms colloidal with soil particles, usually with a thickness of a few millimeters to a few
39 centimeters (Weber et al., 2022). Biocrusts occupy a wide range of ecological niches in mid
40 latitudes, polar and alpine regions, covering approximately 11% of the global land area (Porada
41 et al., 2019). In particular, biocrusts are well-adapted to water-limited, nutrient-poor, and hostile
42 environments, such as arid and semi-arid areas characterized by low ratios of precipitation to
43 potential evaporation ($0.05\text{-}0.5\text{ mm mm}^{-1}$) (Pravalie, 2016; Read et al., 2014; Weber et al., 2016).

44 As vital components of dryland ecosystems, biocrusts fulfill many essential ecological
45 functions. They contribute to stabilizing the soil surface, improving soil permeability, and
46 enhancing water-holding capacity within the upper few centimeters of soil (Sun et al., 2023;
47 Shi et al., 2023; Gao et al., 2017). By participating in various biogeochemical cycles, biocrusts
48 were estimated to contribute to 15% of terrestrial net primary productivity and 40-85% of
49 biological nitrogen fixation (Elbert et al., 2012; Rodriguez-Caballero et al., 2018). They also
50 impact ecohydrological processes by altering soil microclimate and redistributing soil water
51 (Kidron et al., 2022; Tucker et al., 2017). Moreover, biocrusts influence seed capture and soil
52 seed banks (Kropfl et al., 2022), thereby mediating plant growth and community assembly
53 (Havrilla and Barger, 2018; Song et al., 2022). The extent and magnitude of these ecological
54 functions and services depend on the spatial distribution of biocrusts. Therefore, it is crucial to
55 understand their distribution.

56 Despite the significance of biocrusts, previous studies have primarily focused on their
57 contributions to carbon and nitrogen cycling across various habitats and climates (Hu et al.,
58 2019; Morillas and Gallardo, 2015), as well as interspecific interactions and biocrust
59 biodiversity (Machado De Lima et al., 2021; Munoz-Martin et al., 2019), rather than their
60 spatial distribution. A group of ecologists, including Fernando Maestre (Maestre et al., 2021),
61 David Eldridge (Eldridge and Delgado-Baquerizo, 2019; Eldridge et al., 2023), Matthew
62 Bowker (Qiu et al., 2023), Emilio Rodríguez-Caballero (Rodríguez-Caballero et al., 2018) and
63 others, have actively promoted progress in the field (Fig. 1a). Countries with extensive dryland

64 areas, such as China, the United States, Spain, the United Kingdom, Germany, Australia, and
 65 Israel, have attempted to make breakthroughs on this issue. (Fig. 1b). However, other dryland
 66 countries and regions, such as central and southern Africa, where the biocrust distribution has
 67 been reported, still suffer from a paucity of studies and data on biocrusts (Fig. 1c). This
 68 geographical imbalance in biocrust distribution studies has resulted in most knowledge
 69 remaining at local to regional scales, with very limited discoveries on a global scale.



70

71 Fig. 1 Literature review of biocrust distribution studies. (a) Representative authors associated
72 frameworks for biocrusts distribution studies (1990 to 2022). The time series is the average
73 time of the year of publication, e.g., if the number of articles is 2 in 2004 and 8 in 2019, the
74 node in this figure shows the year as $(2004 \times 2 + 2019 \times 8)/10 = 2016$. (b) Map of hotspot
75 countries for biocrust distribution research, with the top 12 countries in terms of number of
76 publications shown; The database is Web of Science, TS = ("biogenic crust*" OR "biological
77 crust*" OR "biological soil crust*" OR "biocrust*" OR "microphytic crust*" OR "microbiotic
78 crust*" OR "cyanobacterial*" OR "algal*" OR "lichen*" OR "moss*" OR "biotic crust*") AND
79 ("mapping*" OR "distribution*" OR "spatial pattern*") AND ("dryland" OR "hyper*arid*" OR
80 "arid*" OR "semi*arid*" OR "dry subhumid*"), with research interests in Environmental
81 Sciences/Ecology and a total of 700 papers. (c) Global biocrust data distribution, based on field
82 surveys and literature compilation. Data have been collected and expanded from the published
83 database (Chen et al., 2020; Rodriguez-Caballero et al., 2018) to 3848 items.

84 In this study, we aimed to sort out and advance the understanding of biocrust distribution
85 from three perspectives: the applicability and comparison of research methods (section 2),
86 clarification of factors influencing biocrust distribution (section 3), and challenges and
87 strategies for future studies on biocrust distribution (section 4). This work is expected to deepen
88 our understanding of dryland ecosystem processes and provide a scientific basis for conserving
89 dryland ecosystems and their responses to global change.

90 **2. Research Methods**

91 Three methods are commonly used to study biocrust distribution: spectral characterization,
92 vegetation dynamic modeling, and geospatial modeling. This section provides an overview of
93 these methods, including their basic principles, case studies, adaptability, and limitations.

94 **2.1 Spectral characterization index**

95 With advances in remote sensing and geo-information technology, spectroscopy offers a
96 feasible method of characterizing distribution features from a physical point of view.
97 Differences in absorption or reflection of specific wavelengths by different ground covers can
98 effectively identify soil surface objects (Rodriguez-Caballero et al., 2015). By identifying
99 biocrust-specific bands from reflectance spectral images (Karnieli et al., 1999), it is possible to

100 construct a presence-absence map of biocrust distribution (Fig. 2a).

101 Currently, spectral characterization indices have been widely applied in many areas of
102 drylands. For example, cyanobacterial biocrusts are widely distributed in the Sahara region of
103 Africa (Beaugendre et al., 2017) and the Negev Desert of Israel (Panigada et al., 2019), where
104 the study inverted the Biocrust Index (CI) based on remotely sensed imagery to access the
105 characteristics of localized changes in biocrust distribution over 31 years (Karnieli, 1997; Noy
106 et al., 2021). Sun et al. (2024) developed the fraction biocrust cover index (FBCI) based on
107 radiative transfer and mapped biocrust distribution over a desert area at 10 m resolution,
108 showing well-matched results between the model and field observations (RMSE of 0.0774,
109 systematic deviation of -4.05%). In the Gurbantunggut Desert, a study constructed the
110 Biological Soil Crust Index (BSCI) with lichen biocrust as the dominant group and mapped the
111 distribution of biocrusts with high accuracy (accuracy of 94.7%, kappa coefficient of 0.82)
112 (Chen et al., 2005), spatially, biocrusts cover 28.7% of the area, with a high and uniform cover
113 in the southern part of the desert and a scattered distribution in other regions (Zhang et al.,
114 2007). In the Loess Plateau, RGB image-based biocrust monitoring showed that variability in
115 biocrusts cover decreased logarithmically with increasing plot size until a critical size of 1m²,
116 after which biocrusts cover remained approximately constant (Wang et al., 2022a).

117 For the spectral characterization method, it is critical to determine the threshold of spectral
118 bands that represent biocrusts. For instance, at an aerosol optical depth of 0.2, the BSCI ranges
119 from 4.13 to 6.23 and narrows to 4.58-5.69 with increasingly poor atmospheric conditions.
120 Overly strict or loose threshold ranges can easily lead to biocrust omission or misidentification.
121 To improve the accuracy of biocrust identification, some researchers have utilized the
122 hyperspectral sensor's continuous waveband capabilities and created the Continuum Removal
123 Crust Identification Algorithm (CRCIA) (Chamizo et al., 2012b; Weber et al., 2008). Baxter et
124 al. (2021) innovatively applied the random forest algorithm to spectral feature classification,
125 achieving an accuracy of 78.5% in biocrusts recognition. Additionally, two other indices, the
126 Sandy Land Ratio Crust Index (SRCI) and the Desert Ratio Crust Index (DRCI), were
127 introduced to account for differences between sandy land (vegetation cover FVC <20%) and
128 desert environments, improving mapping accuracy by approximately 6% (Wang et al., 2022b).

129 The spectral characterization method is easy to use and, thus, facilitates access to
130 continuous long-term dynamics of biocrusts distribution. However, mosses and vascular plants
131 are generally mixed up in this method because their reflectance characteristics are similar across
132 all wavelengths, especially when mosses are wet, which makes them indistinguishable (Fang
133 et al., 2015). Therefore, the spectral characterization method mainly applies to situations where
134 biocrust cover is greater than 30% and plant cover is less than 10% (Beaugendre et al., 2017).
135 It should be noted that the existing indexes mostly correspond to biocrusts cover consisting of
136 specific dominant groups in specific environments, which cannot be directly extrapolated to
137 areas with highly heterogeneous environments (Table 1). Wetting or disturbance may also lead
138 to large fluctuations in the reflectance of different land types, interfering with biocrust
139 distribution monitoring (Rodriguez-Caballero et al., 2015; Weber and Hill, 2016).

140 **2.2 Dynamic global vegetation models (DGVMs)**

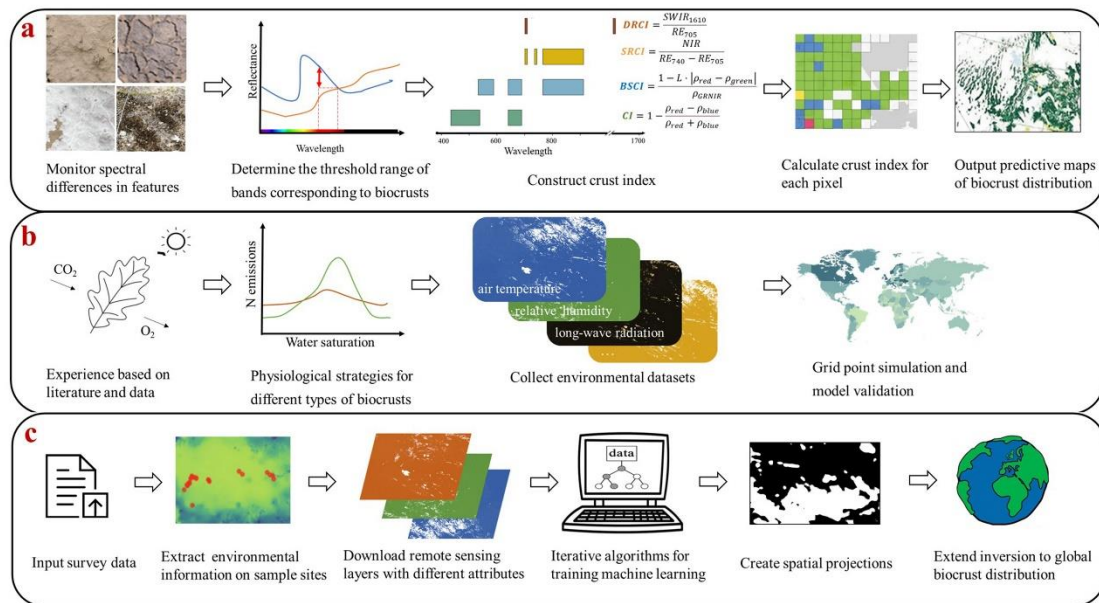
141 Dynamic global vegetation models are another major method for estimating vegetation
142 cover (Deng et al., 2022). These models mainly focus on simulating the biogeochemical
143 processes (e.g., carbon and water cycles) and the metabolic and hydrological processes of
144 organisms (Fig. 2b) (Lenton et al., 2016; Porada et al., 2017). DGVMs have significant
145 advantages in mapping biocrust distribution because their assumptions have clear biological
146 implications (Cuddington et al., 2013). Porada et al. (2013) focused on CO₂ diffusion rates and
147 photosynthetic processes under dynamic water content saturation in dryland biocrusts. By
148 parameterizing long-term climate data and disturbance intervals and averaging simulation
149 results for the past 20 years for each grid point, they estimated that biocrusts cover 11% of the
150 global terrestrial land surface (Fig. 3a) (Porada et al., 2019). Specifically, the light and dark
151 cyanobacteria were widely distributed in deserts, savannas, grasslands, and Mediterranean
152 woodlands at low latitudes, with their presence increasing to some extent with increasing
153 dryness. In contrast, mosses were mainly distributed in middle and high latitudes and polar
154 regions.

155 Dynamic vegetation models can be combined with cross-scale remotely sensed data to
156 quantify the geographic distribution and biogeochemical effects of plants, replacing traditional
157 measurements. However, the uneven distribution density of biocrust data points along the

158 aridity gradient or a small amount of data may lead to poor prediction of global-scale
159 distributions (Quillet et al., 2010). So far, non-vascular vegetation has not received enough
160 attention, and only the Lichen and Bryophyte Model (LiBry) used in the above case is uniquely
161 suited to emulating biocrust distribution (Porada et al., 2019; Porada et al., 2013). The LiBry
162 model includes variations in biocrust cover strategy under disturbance and its growth, but it
163 relies heavily on subjective experience and model parameterization, which is still immature
164 compared to dynamic models of vascular vegetation.

165 **2.3 Geospatial models**

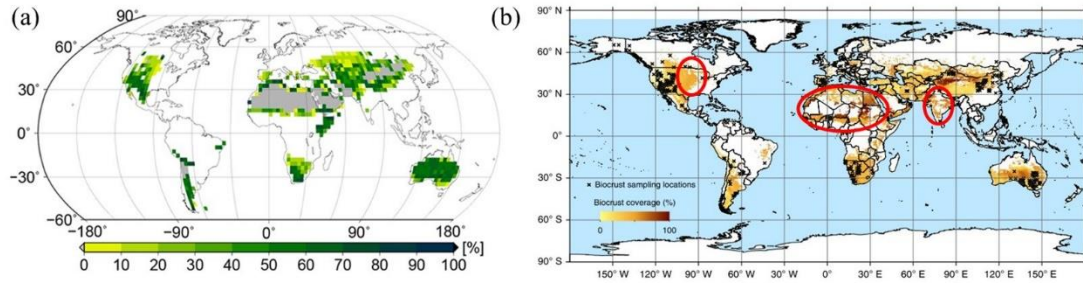
166 Directly relating vegetation presence or cover to environmental data, instead of indirectly
167 via biological processes, is another important way to obtain biocrust distribution (Beaugendre
168 et al., 2017; Fischer and Subbotina, 2014; Skidmore et al., 2011). Classic statistical models can
169 serve this purpose. However, they still require comprehensive expert knowledge of how
170 environmental factors affect biocrusts (Pearce et al., 2001), which is hard to obtain and prone
171 to bias. Geospatial models, which integrate machine learning tools with field survey data and
172 remote sensing data, hold the most promise (Fig. 2c) (Crego et al., 2022). They are also known
173 as species distribution models or ecological niche models (Brown and Anderson, 2014;
174 Jiménez-Valverde et al., 2008; Soberon and Nakamura, 2009). At the global scale, there has
175 been only one study that predicted biocrust distribution patterns using geospatial modeling
176 (Rodríguez-Caballero et al., 2018), which found that biocrust covers 12.2% of the global land
177 surface area, which is about 1.79×10^7 km² (Fig. 3b).



178

179 **Fig. 2** Summary of three major approaches to studying biocrust distribution. Illuminations of
 180 applying spectral characterization method **(a)**, dynamic vegetation model **(b)**, and geospatial
 181 model **(c)** in biocrusts distribution study. See the main text for a more detailed introduction to
 182 these methods.

183 Compared with the result of the dynamic vegetation model, the simulation accuracy
 184 ($R^2 \sim 0.8$) and mapping resolution ($0.5^\circ \times 0.5^\circ$) of the geospatial model were improved.
 185 Biocrust distribution is generally consistent in the large deserts of Asia, western America,
 186 Europe, and Oceania, while some semi-arid regions, such as the northern and southern margins
 187 of the African Sahara Desert, South Asia, and central North America, have significantly higher
 188 biocrust cover in the projection by Rodriguez-Caballero et al. (2018). We estimate that this may
 189 be because geospatial modeling focuses more on the influence of climate, as the Mediterranean
 190 climate and tropical desert climate in the Sahara Desert, as well as the tropical desert climate
 191 of northwestern South Asia, are suitable for biocrust survival. Additionally, the large number
 192 and high cover of biocrust training sets in central North America could have contributed to the
 193 generally high predicted cover in machine learning.



194

195 **Fig. 3** Maps of global biocrusts distribution. (a) Prediction based on vegetation dynamic model
 196 (Porada et al., 2019). (b) Prediction based on geospatial model (Rodriguez-Caballero et al.,
 197 2018).

198 As black-boxes, geospatial models are largely non-interpretable and, thus, less capable of
 199 capturing the key mechanisms behind phenomena, which may limit their applications. Under
 200 this methodological framework, only the direct effects of various environmental indicators are
 201 considered. For example, it focuses on the direct effect of precipitation on biocrust distribution
 202 while ignoring the indirect effects, such as interactions among shrubs, grasses, and biocrusts
 203 (Wang et al., 2024). In addition, to avoid confounding model predictions, the inclusion of
 204 environmental factors should be based on their relevance to biocrusts, and expert knowledge
 205 should still be needed to a certain degree (Mäkinen et al., 2022). Not only natural conditions
 206 such as climate, topography, and soil, but also data on human activities such as afforestation,
 207 trampling, and population density need to be considered as environmental indicators in the
 208 model. It should be noted that the superimposition of environmental layers of different
 209 resolutions may cause deviations in results to some extent, which is unavoidable (Zhao et al.,
 210 2024). Despite the above limitations of geospatial modeling, with sufficient computing power,
 211 observation data of biocrust distribution, and suitable environmental information, geospatial
 212 models are supposed to be relatively optimal solutions for predicting biocrust distribution
 213 (Table 1).

214 **Table 1** Comparison among the three main types of methods to predict biocrust distribution

	Spectral characteristic index	Vegetation dynamics model	Geospatial model
Principle	Differences in wavelength reflectance of surface features	Differences in the physiological processes of different biocrust	Remote sensing information-driven and survey data-based

		types	machine learning framework
Advantages	Convenience and ease of use	Clear ecological significance	Machine training simulation, without subjective interference
Disadvantages	Reflectivity is affected by climate change, disturbances; Mosses and vascular plants have similar reflectance characteristics; The results only show the presence or absence of biocrusts without coverage	Experience-based promotion with significant human intervention; Experiments need to be supported by big data	A large amount of computing power; Adequate number of sample points to support accuracy
Applicable scales	Regional scale (Desert and sandy land with <20% vegetation cover)	Regional scale Global scale	Regional scale Global scale

215

216 **3. Influencing Factors of Biocrust Distribution**

217 It is of great importance to clarify the environmental variables associated with biocrust
218 distribution. On the one hand, it helps to frame the range of data selection before modeling and
219 on the other hand, it aids in identifying patterns of biocrust distribution in the context of
220 dynamic changes and various types of environmental information, thereby facilitating the
221 prediction of distributed evolution on longer time scales. Numerous modelling studies (Kidron
222 and Xiao, 2023; Li et al., 2023; Rodriguez-Caballero et al., 2018) have demonstrated that, on
223 the global scale, biocrust distribution is mainly influenced by water conditions, temperature,
224 soil properties, fire and disturbance (Bowker et al., 2016).

225 *Water conditions.* In general, total precipitation (Fig. 4b) is considered to be critical in
226 determining the distribution of biocrusts (Eldridge and Tozer, 1997). Increased precipitation
227 can lead to higher levels of lichen and moss cover, while algal cover may initially increase and
228 then decrease (Budel et al., 2009; Marsh et al., 2006; Zhao et al., 2014). It should be noted that

229 precipitation can also promote the growth of vascular plants, and continuous high cover of
230 vascular plants and litterfall will limit the space available to biocrusts (Bowker et al., 2005). In
231 addition to the total amount of precipitation, the seasonality and frequency of precipitation
232 cannot be ignored (Budel et al., 2009). Winter precipitation and/or smaller rain events benefit
233 biocrusts, especially when mean annual precipitation is less than 500 mm. Meanwhile, a high
234 frequency of precipitation can lead to the dominance of biocrusts over vascular plants (Chamizo
235 et al., 2016; Jia et al., 2019). Experimental evidence shows that precipitation events of 5 mm
236 are able to maintain normal physiological and ecological functions of the biocrust on the
237 Colorado Plateau, USA, while ever lower precipitation events of 1.2 mm can rapidly kill moss
238 biocrust (Reed et al., 2012). Non-precipitation water input is another important water resource
239 type. The Namib Desert receives little rainfall, but lichens and moss biocrusts can reach a
240 relatively high cover (~70%) (Budel et al., 2009). This is because local water vapor tends to
241 condense into fog or dew, which facilitates the survival of three-dimensional species (such as
242 leafy lichens) by trapping air moisture (Eldridge et al., 2020; Kidron, 2019; Li et al., 2021).
243 Similarly, lichen biocrusts are widely distributed in the western U.S. along the Mexican coast
244 due to the high air humidity (dew formation for almost 1/3 of the year) (Mccune et al., 2022;
245 Miranda - González and Mccune, 2020).

246 *Temperature.* Relatively high soil temperature can create an environment of high
247 evaporation that impedes biocrusts colonization (Garcia-Pichel et al., 2013). Regarding air
248 temperature, warming by 4°C could alter biocrust community structure, resulting in a sharp
249 decrease in moss biocrust cover and an increase in cyanobacterial biocrust cover. This effect
250 becomes even more significant when warming interacts with time and precipitation treatments
251 (Ferrenberg et al., 2015). Recent studies have shown that historical and future temperature
252 changes also affect biocrust distribution. For example, the climate legacy over the last 20,000
253 years could indirectly affect the distribution and relative species richness of biocrusts by
254 altering vegetation cover and soil pH (Eldridge and Delgado-Baquerizo, 2019). Additionally,
255 under future scenarios of increased temperature and aridity, biocrust cover is predicted to
256 decrease by approximately 25% by the end of the century, with communities shifting towards
257 early cyanobacterial biocrusts (Rodríguez-Caballero et al., 2022).

258 *Soil properties.* For a long time, it was commonly believed that finer soils benefit biocrust
259 growth (Belnap et al., 2014; Williams et al., 2013). However, some scientists have challenged
260 this notion (Fig. 4c). For example, Kidron (2018) argued that soils with high dust or fine grains
261 are not a necessary condition for biocrust distribution. Qiu et al. (2023) suggested that soils
262 with small amounts of gravel (0.04-22.34% content, 0.58% being optimal) are more favorable
263 for biocrusts. Another study has shown that the soil parent material determines the degree of
264 surface weathering and the water-holding capacity of the soil, thus indirectly influencing the
265 distribution of biocrusts (Bowker and Belnap, 2008). Gypsum or calcareous soils tend to
266 develop mosses and lichens (Elbert et al., 2012), while sandy soils tend to develop
267 cyanobacteria (Root and Mccune, 2012).

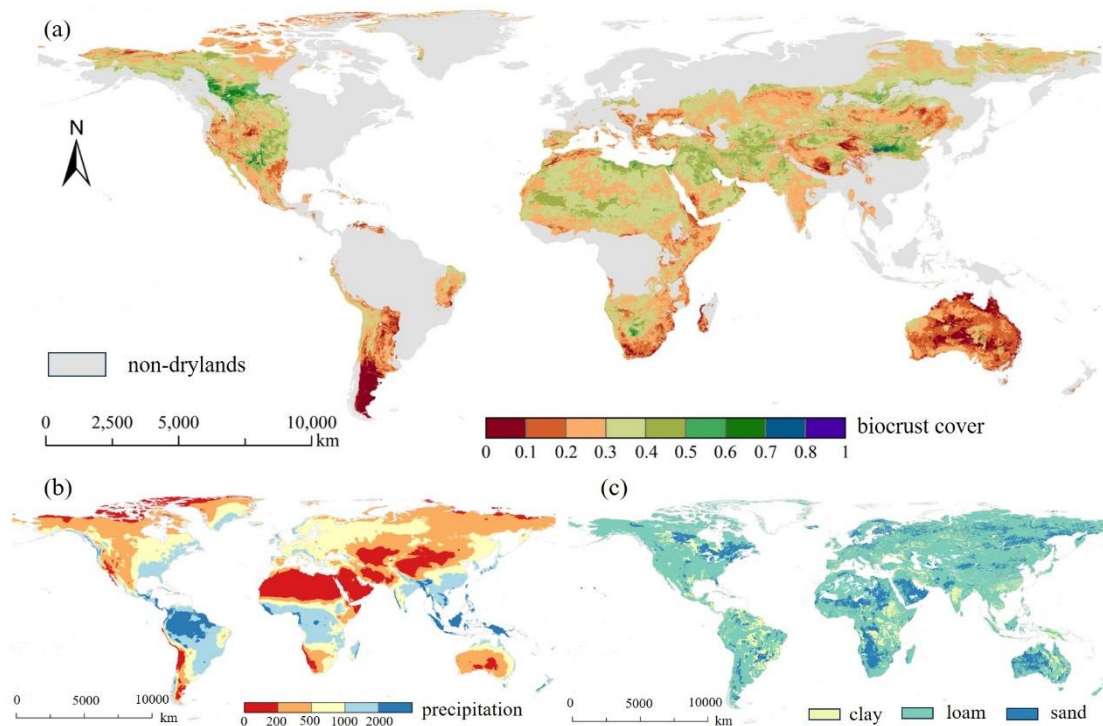
268 *Fire.* Grassland is a major life form in dryland ecosystems, making it crucial to explore
269 the effects of fire events on biocrust distribution (Palmer et al., 2022). Fire-induced soil
270 warming can alter the resource allocation and dynamic growth mechanisms between biocrusts
271 and vascular plants (McCann et al., 2021), potentially leading to a reduction in species richness
272 and cover of biocrusts, especially cyanobacteria, and algae (Abella et al., 2020; Palmer et al.,
273 2020). (Condon and Pyke, 2018) showed that moss cover increases with time after the fire, with
274 no significant change in lichen cover.

275 *Disturbance.* Activities such as grazing, agricultural practices, and land development can
276 significantly impact biocrust distribution. Studies have demonstrated that grazing intensity can
277 lead to substantial changes in biocrust cover. For instance, in Patagonian rangelands, biocrust
278 cover decreased by 85%, 89%, and 98% under light, medium, and heavy grazing, respectively
279 (Velasco Ayuso et al., 2019). In the Loess Plateau, total biocrust cover remained almost
280 unchanged under light grazing (< 30.00 goat dung / m²), but there were variations in community
281 structure, with an increase in cyanobacteria biocrusts (23.1%) and a decrease in moss biocrusts
282 (42.2%) due to reduction in vascular plant cover (Ma et al., 2023). Tillage practices can disrupt
283 the soil surface, leading to a reduction in biocrust cover (6% on average) and diversity, with
284 lichens struggling to survive in tilled fields compared to mosses (Durham et al., 2018).
285 Additionally, late-successional biocrusts exhibit higher tolerance compared to pre-successional
286 biocrusts. Moss biocrusts, for instance, can maintain soil microbial biomass and nematode

287 abundance better under trampling disturbance compared to cyanobacteria and lichen biocrusts
288 (Yang et al., 2018). However, contrary to this view, it has been observed that cyanobacterial
289 biocrusts increased in cover from 81% to 99% after trampling, while lichen and moss biocrusts
290 decreased from 1.5% and 18% to less than 0.5%. Furthermore, mining activities can
291 significantly reduce the photosynthetic potential of biocrusts, particularly affecting the recovery
292 of cyanobacterial biocrusts (Gabay et al., 2022).

293 *Other factors.* On a global scale, biocrust distribution is also closely linked to
294 biogeographic isolation. Strong spatial heterogeneity, accompanied by spatial distance, can
295 create barriers to the dispersal of propagules (spores, fungal bodies), which indirectly impedes
296 colonization of the biocrusts (Garcia-Pichel et al., 2013). In addition, factors such as vascular
297 plant cover, topography, and solar radiation also influence biocrust distribution. albeit to a lesser
298 extent than the factors mentioned above. For further insights, readers are encouraged to consult
299 Chapter 10 of *Biological Soil Crusts: An Organizing Principle in Drylands*, which provides an
300 overview of the control and distribution patterns of biocrusts from micro to global scales
301 (Bowker et al., 2016).

302 To sum up, climate is the most important factor influencing global biocrust distribution,
303 especially in drylands where water is precious to the organisms. However, exploration of the
304 roles of climatic factors such as rainfall seasonality and atmospheric drought still needs much
305 further effort (Wright and Collins, 2024), especially in the context of global climate change.
306 Although more attention has been paid to the physical properties of soils, the roles of their
307 chemical properties, such as the nitrogen (N) and phosphorus (P) content, need to be taken
308 more seriously. Fire and disturbance are usually ignored. However, due to the trend towards
309 warmer and drier environments, as well as increasing population and the need to sustain
310 livelihoods, their influences on biocrust distribution may become more important. As one of
311 the basic processes on a global scale, biogeographic isolation or changes in land use should be
312 paid more attention to. With the increasing number of biocrust data points, we can expect this
313 aspect will see a surge in research.



314 Fig. 4 Biocrust distribution and its critical influencing factors. (a) Biocrust cover map and its
 315 influencing factors. (a) Global biocrust distribution, by random forest modelling. Based on a
 316 global biocrust database constructed by Chen et al., we expanded the biocrust data to 3848
 317 entries through literature compilation and field surveys and fitted them with four types of
 318 remotely sensed environmental data, including climate, land use, soil properties, and elevation,
 319 to finally predict the suitable areas for the biocrust distribution and quantify the biocrust cover.
 320 (b) Global average annual precipitation (1970-2020), data from the WorldClim database
 321 (version 2.1). (c) Global soil texture distribution, data from HWSD (Harmonized World Soil
 322 Database, version 1.2). Precipitation and soil texture were taken as examples of environmental
 323 factors.

324 4. Challenges and Perspectives

325 Biocrusts play a crucial role in dryland ecosystems, making it essential to understand their
 326 current status and distribution dynamics. For influencing factors (Chapter 3), traditional
 327 observational studies and controlled experiments offer multiple perspectives of foundational
 328 knowledge. For assessing biocrust distribution patterns (Chapter 2), the methods shift from
 329 traditional approaches to spectral index, vegetation dynamics, and geospatial models that span
 330 multiple subjects like ecology, biology, geology, and computer science. However, high-

331 precision biocrust distribution data across geographic units remain scarce, and current research
332 methods are still limited. To further advance studies of biocrust distribution, we propose the
333 following aspects for consideration.

334 **5.1 Building standardized biocrusts database**

335 Currently, biocrust data are fragmented, low in volume, and derived from narrow sources,
336 largely limiting spatial prediction from points to broader areas. Thus, we suggest that a global
337 effort to build a standardized and specialized biocrusts database. This database should include
338 consistent data items (such as main types and cover of biocrusts, latitude, longitude, and cover)
339 and adhere to uniform inclusion criteria. Such a database is an important infrastructure for
340 mapping global biocrust distribution, serving as the benchmark for training and validating
341 spectral characteristics, DGVM, and geospatial models (Engel et al., 2023). Given the difficulty
342 of conducting field surveys worldwide, compiling biocrust data from the published literature
343 or other sources would be a primary approach (Fig. 4(a)). To date, several published studies
344 have assembled 900 ~ 1,000 data on biocrust presence or absence from the literature (including
345 584 data on biocrust cover) (Chen et al., 2020; Eldridge et al., 2020; Havrilla et al., 2019;
346 Rodriguez-Caballero et al., 2018). However, compiling from literature largely comes to its
347 limitations and is still far from building a standardized and specialized biocrusts database.
348 While open databases are not specialized to biocrusts, some of them may provide valuable
349 additions (Fig. 5). For instance, the biodiversity and specimen datasets such as GBIF and the
350 Atlas of Living Australia (Belbin and Williams, 2015; García-Roselló et al., 2015) contain a
351 large amount of information on species, including mosses and lichens (Table 2), potentially
352 offering hundreds or even thousands of entries of biocrusts occurrence or cover. Similarly,
353 global, national, and regional plant flora can significantly contribute to building the
354 standardized and specialized biocrusts database. For example, sPlot includes ~2 million
355 vegetation plot data (Sabatini et al., 2021), and the European Vegetation Archive (*EVA*) also
356 holds 1.6 million entries over the globe or Europe (Chytrý et al., 2016). Regional datasets like
357 the Environmental Monitoring of Arid and Semiarid Regions (*MARAS*) have surveyed 426 sites
358 (up to September 2020) and provided regular access to 624.50 km² of rangeland vegetation
359 spatial patterns, species diversity, soil functional indices, climatic data, and landscape

360 photographs in the Patagonia region of Argentina and Chile (Oliva et al., 2020). Concerns about
 361 land use products are also necessary. Global land use maps, based on the PROBA-V sensor,
 362 which contain spatial information for the Moss & Lichen layer, have an annual update
 363 frequency and a resolution of 100 m. Additionally, an increasing number of amateurs contribute
 364 significantly to global species information entries through species identification apps, which
 365 are user-friendly and widely accessible. The citizen science project *iNaturalist* is a very good
 366 example (Wolf et al., 2022). Furthermore, when collecting and collating data from non-
 367 academic sources, the combination of web crawlers and text analysis can help in obtaining
 368 biocrusts data and addressing key ecological issues.



369
 370 **Fig. 5** Potential approaches to building a standardized biocrusts database. (a) Distribution of
 371 lichens in the GBIF database with an example photo, (b) environmental monitors distribution
 372 map of MARAS database, (c) distribution of "mosses and lichens" in the PROBAV_LC100
 373 database (light yellow area) in northern Asia, for instance.

374 **Table 2** References for biocrusts database expansion channels

375

376

5.2 Improving non-vascular vegetation dynamic models

Data type	Data source	Extend	Biocrust type	Georeferenced records	Presence	Coverage	Link
Biodiversity data	the Global Biodiversity Information Facility(GBIF)	Worldwide	Cyanobacteria	~780000	✓	--	https://www.gbif.org/
			Lichen	~19000			
			Moss	~90000			
	Atlas of Living Australia(ALA)	Australia	Cyanobacteria	~53000	✓	--	https://www.ala.org.au/
			Lichen	~12000			
			Moss	~20000			
	Chinese Virtual Herbarium	China	Moss and lichen	--	✓	--	https://www.cvh.ac.cn/
			Lichen	~2000	✓	--	https://plants.jstor.org/
	Global Plants on JSTOR	Worldwide	Moss	~480			
			All	--	✓	--	https://www.inaturalist.org/
Citizen Science Survey data	MARAS	Argentina and Chile	All	426	✓	✓	https://springernature.figshare.com/collections/The_MARAS_dataset_vegetation_and_soil_characteristics_of_dryland_rangelands_across_Patagonia/4789113
		Worldwide	Lichen	6801	✓	✓	https://www.idiv.de/en/splot.html
	sPlot	Worldwide	Moss	11001	✓	✓	
			Non-vascular plants	6623	✓	✓	https://edgg.org/databases/GrassPlot/
Landcover data	Vegbank	Canada and the United States	Moss and lichen	~15000	✓	✓	http://vegbank.org/
		The United States	Moss and lichen	5200	✓	✓	https://gbp-blm-egis.hub.arcgis.com/pages/aim
	BLM_AIM	Australia	All	~300			http://www.aekos.org.au/
			Worldwide	Moss and lichen	--		

377 There are only two DGVMs applicable to non-vascular organisms – LiBry and ECHAM6-
378 HAM2-BIOCRUST (Rodriguez-Caballero et al., 2022). Despite their utility, these models still
379 require performance improvements. Future directions for enhancing these models could include
380 incorporating spatial self-organization of non-vascular organisms (Gassmann et al., 2000), the
381 effects of fire (Thonicke et al., 2001), vegetation-environment feedback processes (Quillet et
382 al., 2010), functional traits (Boulangeat et al., 2012), intraspecific-interspecific interactions
383 (Boulangeat et al., 2014) and seasonal dynamics. Moreover, the physical properties,
384 photosynthetic capacity, and carbon and nitrogen allocation of biocrusts change along
385 environmental gradients in complex and context-dependent ways. These factors should be
386 incorporated into DGVMs (Fatichi et al., 2019). Spatial-explicit DGVMs may be one key to
387 effectively improving the accuracy of simulations in future studies, although they are data-
388 intensive. Also, biocrusts are significantly influenced by hydrological processes and, in turn,
389 affect these processes (Chen et al., 2018; Whitney et al., 2017). However, ecohydrological
390 models, which focus on hydrological processes are rarely connected to global biocrust
391 distribution predictions. (Jia et al., 2019) attempted to incorporate biocrusts cover as a system
392 state variable in an ecohydrological model, investigating biocrusts cover under varying rainfall
393 gradients. By feeding ecohydrological models with global environmental data, particularly
394 hydrological variables, these models could offer a new approach to predicting biocrust
395 distribution on a global scale.

396 **5.3 Integrated application of high-quality sensors**

397 The spectral characterization method lies in the differences in spectral reflectance of
398 biocrusts and other land types at various wavelengths. Consequently, the accuracy of the results
399 is contingent on the quality of the sensors used. Previous studies often employed a single sensor
400 with fixed band intervals for distinguishing biocrusts, potentially missing critical spectral
401 features of different land types (Chamizo et al., 2012a). If the biocrusts index can be constructed
402 by combining and comparing the full-band spectral data from multiple terrestrial sensors and
403 infrared cameras, and other devices, the errors will be reduced to a certain extent, thus
404 improving the classification accuracy (Wang et al., 2022b). In addition, the unique advantages
405 of hyperspectral data, which include large data volumes and narrow bands, allow for the

406 development of new biocrust discrimination standards when combined with observational data.
407 If further estimation of biocrust cover can be achieved on this basis, it will be a significant
408 contribution to the study of large-scale biocrust distribution (Rodríguez-Caballero et al., 2017).
409 To date, high-resolution sensors have proven successful in monitoring lichens and mosses
410 (Blanco-Sacristan et al., 2021), and the release of such products is something important to look
411 out for in the future.

412 **5.4 Making full use of machine learning**

413 Machine learning can be combined with remote sensing products to uncover complex
414 features from big data, enabling the prediction of global biocrust distribution (Collier et al.,
415 2022). This data-driven approach has powerful predictive capabilities, especially for mapping
416 species distribution, and can largely avoid the errors of missing or misidentifying biocrusts
417 caused by traditional methods (relying on field measurements to determine threshold ranges)
418 (Wang et al., 2022b). In the remote sensing image classification, mature machine learning
419 algorithms include support vector machines, single decision trees, random forests, artificial
420 neural networks, etc. (Yu et al., 2020). Ensemble models combining multiple algorithms have
421 been widely used in the field of species distribution, but have seen relatively few applications
422 in biocrust prediction. In the future, using machine learning to identify parameters for dynamic
423 models of biocrusts may be one of the most promising methods to predict biocrust distribution
424 (Perry et al., 2022).

425 **5.5 Regional research synergy development**

426 Research on biocrust distribution has shown significant spatial and climatic imbalances.
427 The study areas that have been conducted are relatively concentrated in countries such as China,
428 the United States Spain, Australia, and Israel. Although there are large areas of dryland
429 distributed in Africa (other than South Africa), central Asia, central South America, and
430 northern North America, research on biocrusts in these regions is scarce. These unbalanced
431 regional research efforts constraint the advancement of studies on global biocrust distribution.
432 Therefore, how to coordinate and promote the common progress of regional research is an
433 urgent issue at present. Climatically, in addition to the drylands, the cold zones may be another
434 important area to explore biocrust distribution (Pushkareva et al., 2016). On the Tibetan Plateau,

435 studies have investigated the spatial variation of different types of biocrust communities across
436 climatic gradients and their effects on soil temperature features and freezing duration (Ming et
437 al., 2022; Wei et al., 2022). These findings highlight the need for more studies on biocrust
438 distribution in the alpine areas.

439 **5. Conclusion**

440 Biocrusts are of great significance to the ecohydrological processes, soil material cycling,
441 landscape shaping, and biodiversity conservation in drylands. To date, numerous studies have
442 tried to fill the knowledge gap in biocrust distribution at the regional scale. However, global-
443 scale research remains scarce, and mapping accuracy is still insufficient, directly leading to
444 ambiguities in ecological function assessment and prediction. Therefore, advancing global-
445 scale biocrust distribution research requires a more comprehensive consideration of the
446 applicability of previous methods and a broader knowledge base to help select environmental
447 indicators. For future work in this field, we advocate for closer cooperation among scientists to
448 build a global standardized database incorporating multiple sources of biocrust data. This effort
449 should primarily focus on expanding biocrust data items in understudied regions where
450 biocrusts have been reported, thereby creating a larger, multi-habitat training set. Meanwhile,
451 modern learning tools, such as deep learning, should be broadly applied to high-quality sensor
452 image segmentation, data classification, and model parameter tuning. Finally, long-term
453 monitoring and simulation are necessary to better understand the dynamics of ecological
454 restoration in drylands and the response of biocrusts to environmental changes.

455

456 **Author contribution**

457 Siqing Wang co-conceived the idea, collected data on the biological soil crust, wrote the first
458 draft, prepared the figures, and revised the manuscript. Li Ma, Liping Yang, Yali Ma, and
459 Yafeng Zhang collected data on biological soil crust and revised the manuscript. Changming
460 Zhao co-conceived the idea. Ning Chen co-conceived the idea, collected data on the biological
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462

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469

470 **Competing interests**

471 All authors declare no conflict of interest.

472

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